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# A new species of *Lutreolina* Thomas, 1910 (Marsupialia, Didelphidae) from the Early Pleistocene of the southern Pampas (Buenos Aires Province, Argentina)

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ARTÍCULO

# A NEW SPECIES OF *LUTREOLINA* THOMAS, 1910 (MARSUPIALIA, DIDELPHIDAE) FROM THE EARLY PLEISTOCENE OF THE SOUTHERN PAMPAS (BUENOS AIRES PROVINCE, ARGENTINA)

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**Abstract.** We describe *Lutreolina tonnii* sp. nov. (Mammalia, Metatheria, Marsupialia, Didelphimorphia, Didelphidae), recovered from Early (or Early–Middle) Pleistocene deposits of the coastal cliffs near Necochea City in Buenos Aires Province, Argentina. Its holotype, a right maxillary with M1-3, indicates that it belongs to the largest species of the genus, including extinct and extant species. It also differs from other species of the genus in having more anteroposteriorly compressed protocones in the upper molars. It differs from the living species in that the maxillary-jugal contact is less horizontal in its posterior two-thirds, has a deeper ectoflexus in M3, and has a shallow but distinct internal (lingual) crest linking the bases of stylar cusps B and D in M1-3. The new species is the fourth known up to now for the South American record, and the third for the Plio–Pleistocene of the Pampean Region, thus suggesting a considerable diversity for this genus in mid-latitudes of this continent by the end of the Cenozoic Era.

**Key words.** Marsupialia. Didelphidae. *Lutreolina*. Pleistocene. Buenos Aires Province. Argentina.

**Resumen.** UNA NUEVA ESPECIE DE *LUTREOLINA* THOMAS, 1910 (MARSUPIALIA, DIDELPHIDAE) DEL PLEISTOCENO TEMPRANO DE LA PAMPA AUSTRAL (PROVINCIA DE BUENOS AIRES, ARGENTINA). Se describe a *Lutreolina tonnii* sp. nov. (Mammalia, Metatheria, Marsupialia, Didelphimorphia, Didelphidae) procedente de niveles del Pleistoceno Temprano (o Temprano–Medio) de las barrancas costeras de los alrededores de Necochea, Provincia de Buenos Aires, Argentina. El holotipo, un maxilar derecho con los M1-3, se destaca por su gran tamaño comparado con el de las otras especies, fósiles y vivientes, del género. Difiere también de las restantes especies del género en que los protoconos de los molares superiores están más comprimidos anteroposteriormente. Difiere de las especies vivientes en que el contacto maxilo-yugal es menos horizontal en sus dos tercios posteriores, existe un ectoflexo más profundo en el M3, y en que los M1-3 tienen una cresta interna baja pero diferenciada que conecta las bases de las cúspides estilares B y D. La nueva especie es la cuarta forma extinta hasta ahora conocida para el registro sudamericano y la tercera para el Plio–Pleistoceno de la Región Pampeana, indicando una considerable diversidad para el género hacia fines de la Era Cenozoica en las latitudes medias del continente.

**Palabras clave.** Marsupialia. Didelphidae. *Lutreolina*. Pleistoceno. Provincia de Buenos Aires. Argentina.

IN HIS MOST recent review of the taxonomic diversity of living opossums (Mammalia, Metatheria, Didelphimorphia, Didelphidae), Voss (2022) included two species within the genus *Lutreolina* Thomas, 1910: *L. crassicaudata* (Desmarest, 1804) and *L. massoia* Martínez-Lanfranco *et al.*, 2014. Red opossums, or thick-tailed opossums, as they are known, have the most faunivorous-carnivorous feeding habits of all living didelphids. They are medium-sized (500–800 g; Regidor *et al.*, 1999) and have a weasel-like appearance; they are nocturnal, terrestrial (though they swim very well), and are aggressive predators and active hunters, "...taking a variety of invertebrate and vertebrate prey, including mammals, small birds and their eggs, fish, reptiles, and amphibians." (Smith, 2008, p. 4). An interesting aspect of their strictly South American distribution is that they inhabit peri-Amazonian regions: *L. massoia* lives in premontane and montane forests of the Yungas region in south-eastern Bolivia and north-western Argentina. In turn, *L. crassicaudata* has a disjunct distribution, with northern populations in the Llanos of Colombia, Venezuela, and Guyana, and the remaining ones in open environments from southeastern Brazil to the southern Pampas (Stein & Patton, 2008).

In their taxonomic review of the extinct *Hyperdidelphys* Ameghino, 1904, Goin and Pardiñas (1996) reached three

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conclusions relevant to this study: (1) the Late Pleistocene "*Didelphis*" *lujanensis* Ameghino, 1899 is a probable synonym of *Lutreolina crassicaudata* (see also Goin, 1991); (2) the Early Pliocene "*Didelphis*" *biforata* Ameghino, 1904 is referrable to *Lutreolina*, and (3) *Lutreolina* and *Hyperdidelphys* are sister-groups among the Didelphini, being the former more generalized than the latter. Later, Goin and de los Reyes (2011) reviewed the complex history of fossil representatives of *Lutreolina* and concluded that there are three extinct representatives of this genus: the already mentioned *L. biforata*, the Pliocene (Montehermosan and Chapadmalalan South American Land Mammal Age, SALMAs) *L. tracheia* Rovereto, 1914, and *L. materdei* Goin & de los Reyes, 2011, from the Late Miocene (Huayquerian SALMA) of southeastern Peru. They also described new remains of a large species of *Lutreolina* from Early Pleistocene deposits of southern Buenos Aires Province. However, as the new specimens lack dental remains (crucial for the assignation of most extinct didelphids), they restrained from further taxonomic attempts.

Here we describe a new species of *Lutreolina* from Early Pleistocene deposits outcropping near Necochea, in southern Buenos Aires Province (Fig. 1). We also tentatively refer the previously mentioned specimens of a large *Lutreolina*, from outcrops of the same age and also southern Pampean locations to this new species. Thus, the known diversity of extinct representatives of the genus doubles that of the living ones. The new species is the largest member of the genus so far known and adds one more taxon to the list of relatively small carnivorous metatherians that flourished by the late Cenozoic in South America.

**Abbreviations and conventions. MLP,** División Paleontología Vertebrados, Museo de La Plata, Argentina. **MPC,** Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. **MPH-P,** Museo Municipal de Punta Hermengo, Miramar. **SALMA,** South American Land Mammal Age. **St**, stylar cusps. **M1, M2, M3, M4**, upper molars.

The dental formula of didelphids is assumed to be I/i 5/4, C/c 1/1, P/p 3/3, and M/m 4/4; dP/p3 is the deciduous third premolar. Molar anatomical terminology follows Goin *et al.* (2016). Weight is given in grams (g), angles in degrees (°), and dental measurements in millimeters (mm).

**Figure 1.** Map of central Argentina indicating the fossil locality (red star) were specimen **MLP 01-IV-5-29** (holotype of ***Lutreolina tonnii*** sp. nov.) was found. The coloured region, in light green, indicates the distribution in this region of the living species ***Lutreolina crassicaudata***.

## SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Infraclass METATHERIA Huxley, 1880
Order DIDELPHIMORPHIA Gill, 1872
Family DIDELPHIDAE Gray, 1821
Subfamily DIDELPHINAE Hershkovitz, 1992
Tribe DIDELPHINI Gray, 1821

Genus ***Lutreolina*** Thomas, 1910

***Type species.*** *Lutreolina crassicaudata* Desmarest, 1804. Late Pleistocene, southern and eastern Brazil; Holocene, Pampean Region, Argentina, and southern and Eastern Brazil; Recent, South America.

***Lutreolina tonnii*** sp. nov.
Figure 2.1–2.2

**LSID** urn:lsid:zoobank.org:act:6D424CEA-4576-4A5E-926C-CFA5B8DF168E

**Etymology.** The species name honors Dr. Eduardo P. Tonni, a distinguished colleague of the Museo de La Plata, Argentina, acknowledging his outstanding contributions to South American Paleontology.

**Holotype.** MLP 01-IV-5-29, a fragment of right maxillary with M1-3, posterior alveolus of P3, and anterior alveoli of M4 (Figs. 2.1–2, 3, and 4.5). Collected by Mr. Rubén Lucero and Mr. Rodrigo Obredor in the year 2007.

**Hypodigm.** The type and specimen MLP 01-IV-5-15, a right maxillary fragment with almost complete M1and alveoli of P1-2 and dP3 (Fig. 2.3–4); collected by Amador Rodríguez at Playa Las Delicias (base of the cliff), north of Mar del Plata City (Buenos Aires Province) *circa* 1990.

**Tentatively referred specimens.** MPH-P 070, a skull fragment lacking the rostral portion (Goin & de los Reyes 2011, fig. 3A-D; Fig. 5.1–4), and MLP 01-IV-5-44, an edentulous, posterior fragment of right dentary with the angular process, the ascending ramus and the condyle (Goin & de los Reyes 2011, fig. 4A-C; Fig. 6.1–3). See Goin and de los Reyes (2011) for the provenance and levels of both specimens, which are early Pleistocene in age.

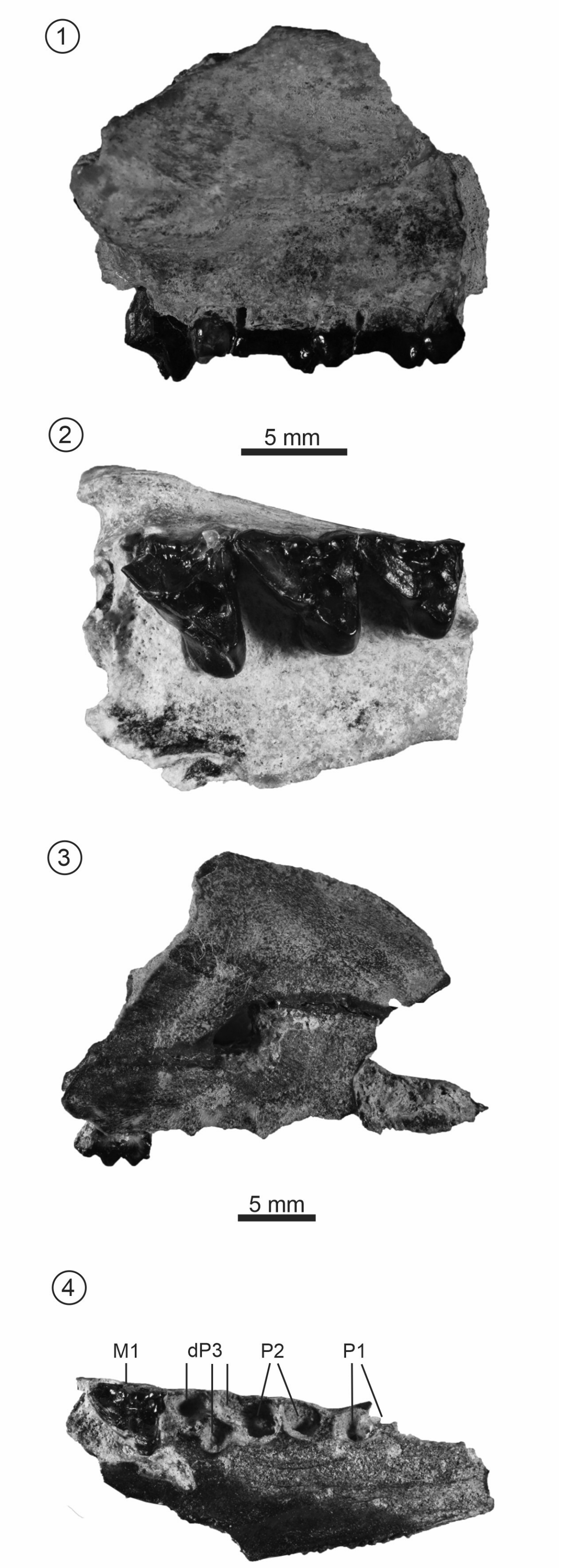

**Figure 2.** ***Lutreolina tonnii*** sp. nov. **1–2, MLP 01-IV-5-29** (holotype), a fragment of right maxillary with M1-3, posterior alveolus of P3, and anterior alveoli of M4. **3–4, MLP 01-IV-5-15**, a right maxillary fragment with almost complete M1 and alveoli of P1-2 and dP3. Indications for P1, P2 and dP3 alveoli are highlighted. Scale= 5 mm.

TABLE 1 – Dental measurements (in mm) of upper molars of *Lutreolina tonnii* sp. nov. and other selected didelphines

| | LM1 | WM1 | LM2 | WM2 | LM3 | WM3 | LM4 | WM4 | LM1-3 | LM1-4 | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lutreolina tonnii* sp. nov. (MLP 01-IV-5-29, holotype) | 4.9 | 4.28 | 5.53 | 5.41 | 5.72* | 6.63 | | 7.01* | 15.50* | 18.50* | This work |
| *Lutreolina tonnii* sp. nov. (MLP 01-IV-5-15) | 5.0 | 4.0 | | | | | | | | | This work |
| *L. crassicaudata*[1] | 3.52 (3.38-3.86) | 2.54 (2.27-2.79) | 3.79 (3.62-3.98) | 3.29 (3.14-3.43) | 3.92 (3.54-4.46) | 3.94 (3.7-4.14) | 1.71 (1.52-1.91) | 4.56 (4.26-4.85) | 10.73 (10.03-11.53) | 12.07 (11.48-13.58) | This work |
| *L. massoia* (MACN 25333) | 3.06 | 2.38 | 3.45 | 2.89 | 3.74 | 3.85 | 1,66 | 4.55 | 9.98 | 11.68 | This work[2] |
| *Lutreolina tracheia* | 3.73 (3.56-3.9) | 2.78 (2.56-3.01) | 3.66 (3.41-3.92) | 3.05 (3.05-3.05) | 3.7 (3.54-3.86) | 5.57 (3.43-4.28) | 1.69 (1.42-1.96) | 5.25 (4.98-5.51) | 10.92 (10.42-11.42) | 12.5 (11.84-13.19) | This work |
| *Hyperdidelphys parvula* | 4.93 (4.21-4.42) | 4.42 (4.04-4.62) | 5.76 (5.12-6.19) | 5.33 (4.95-5.78) | 5.32 (5.2-5.53) | 5.86 (5.45-6.27) | 2.13 (1.98-2.31) | 6.06 (5.86-6.27) | 14.99 (13.52-16.44) | 17.12 (15.5-18.75) | Goin & Pardiñas (1996) |
| *Hyperdidelphys inexpectata* | 5.28 (5.2-5.36) | 4.67 (4.54-4.79) | 5.77 (5.6-5.94) | 5.86 (5.61-6.35) | 5.72 (5.69-5.78 | 6.17 (6.11-6.2) | 2.23 (2.14-2.31) | 6.78 (6.11-8.05) | 17.02 (17.01-17.04) | 19.25 (19.15-19.35) | Goin & Pardiñas (1996) |
| *Hyperdidelphys dimartinoi* | 5.19 (4.75-5.64) | 4.6 (4.38-4.82) | 5.6 (5.53-5.9) | 5.95 (5.90-6.01) | 6.19 (5.9-6.49) | 6.65 (6.57-6.73) | 2.35 (2.25-2.45) | 6.61 (6.51-6.72) | 16.98 (16.18-18.03) | 19.45 (18.43-20.48) | Goin & Pardiñas (1996) |

Measurements in brackets indicate the range obtained from several individuals. The symbol * indicates that the measurement is approximate. In the case of M1-4 length, it should be noted that the M4 of specimen MLP 01-IV-5-29 is lacking and alveoli for this last molar are only partially preserved. Notes: [1] N=4. [2] Measurements obtained with the software ImageJ applied to the figures provided by Martínez-Lanfranco *et al.* (2014).

**Diagnosis.** Largest species of the genus, and much larger than living species. Differs from *L. tracheia* in having proportionally larger StD in M2 and StB and StD in M3; M4 width is larger, judging from the preserved alveoli. Differs from *L. biforata* and *L. materdei* in having upper molars with more anteroposteriorly compressed protocones, as inferred from the corresponding antagonist molars. Differs from living species of the genus in that the maxillary-jugal contact is less horizontal in its posterior two-thirds, has a deeper ectoflexus in M3, has a shallow but distinct internal (lingual) crest linking the bases of StB and StD, and in that the upper molars have more compressed protocones.

**Measurements.** See Tables 1 and 2.

**Geographic and stratigraphic distribution.** The type comes from the base of the coastal cliffs at Punta Negra Beach (38° 39′ S, 58° 56′ W), 16 km SW of Necochea City, Buenos Aires Province, Argentina. Most probably, Early Pleistocene (Ensenadan Stage/Age). However, a Middle Pleistocene age (Bonaerian Stage/Age) cannot be discarded, as younger levels also outcrop at some places of the base of Punta Negra. The basal cliffs at this locality referred to as levels A and B in the profile by Rico and Bidegain (2013: fig. 3; see also Rico *et al.*, 2014: fig. 8) were correlated with the Olduvai Subchron, Matuyama Chron. All other specimens come from Early Pleistocene levels of the southern coast of Buenos Aires Province.

**Description.** The holotype has preserved part of the right maxillary showing the lateral and palatal planes of the bone. Laterally the suture between the jugal and the maxillary bones is mostly horizontally set, bending upwards only at its anterior half (this feature is shared with all species of *Lutreolina*, in contrast to other didelphines). Notwithstanding, it shows a slight step at the midpoint, thus differing from living species. The jugal bone is high and stout. The palatal face of the maxillary extends to the edge of the maxillary fenestra. At its anterior end, the fenestra seems to expand slightly laterally. M1-2 are well-preserved; M3 shows a fissure from the protocone running towards the metastilar edge of the tooth; the distal third of the postmetacrista is lost. The anterior edge of the anterolabial and lingual alveoli for M4 are preserved. From them it can be estimated that the width of M4 (*i.e.*, its labio-lingual diameter) was slightly larger than that of M3; this aspect differs from most known Didelphini (except *Lutreolina* and *Hyperdidelphys*), in which M4 is subequal or slightly smaller in width than M3.

The most distinctive feature of the upper molars of *L. tonnii* is the significant development of the postmetacrista. This crest is oriented at quite an acute angle regarding the dental axis when seen in occlusal view (see the Discussion). This feature, together with the eccentric (anteriorly placed) protocone, gives the upper molars a distinct shape that contrasts with that of most didelphines except *Lutreolina* and *Hyperdidelphys*.

**TABLE 2 – Measurements of M1-4 length (in mm) in *Lutreolina tonnii* sp. nov. and other Didelphinae mentioned in this work**

| Taxon | Length M1-4 | Source |
|---|---|---|
| *Lutreolina crassicaudata* | 12.29 | Martínez-Lanfranco *et al.*, 2014 |
| *Lutreolina massoia* | 10.70 | Martínez-Lanfranco *et al.*, 2014 |
| *Lutreolina tracheia* | 12.20[1] | This work |
| *Lutreolina tonnii* sp. nov. | 18.50[2] | This work |
| *Hyperdidelphys parvula* | 17.12 | Goin & Pardiñas, 1996 |
| *Hyperdidelphys inexpectata* | 19.25 | Goin & Pardiñas, 1996 |
| *Hyperdidelphys dimartinoi* | 20.60 | Goin & Pardiñas, 1996 |

[1] M1-4 length of *L. tracheia* corresponds to the average value of two specimens with complete upper molar series (MPC 4012-3 and MPC 4023-1). [2] See comment in the legend of Table 1.

The stylar region in the type specimen shows a combination of features that is similar to other (extinct and extant) species of the genus *Lutreolina*: absent StC in M1-3 and large, bulbous StB and StD in M1-2, which are close to each other and linked at their lingual bases by a shallow crest.

The anterior cingulum of M1 is vestigial, while that of M2-3 are better developed and more sub-vertically placed than in the living species of the genus. There is no posterior cingulum or pre- and post-protoconal cinguli. The ectoflexus is deeper in M3 than in M1-2. The centrocrista is straight and very short. The preparacrista shows clear signs of wear and in M1-2 forms almost a continuous wear facet with the preprotocrista. In M1-2 there are minute cusps lingual to StD. In M3, StD is much smaller than StB. In M1-3 it can be seen a very small, straight crest that runs posteriorly to StD. The StA is only visible as a distinct cusp in M3; in M2 it is vestigial, while in M1 it is absent. Finally, as in other species of *Lutreolina* and *Hyperdidelphys*, the protocone cusp is highly eccentric in all molars, being placed on the anterolingual edge of the tooth. It is relatively compressed anteroposteriorly, as well as the trigon basin. There are no para- or metaconules.

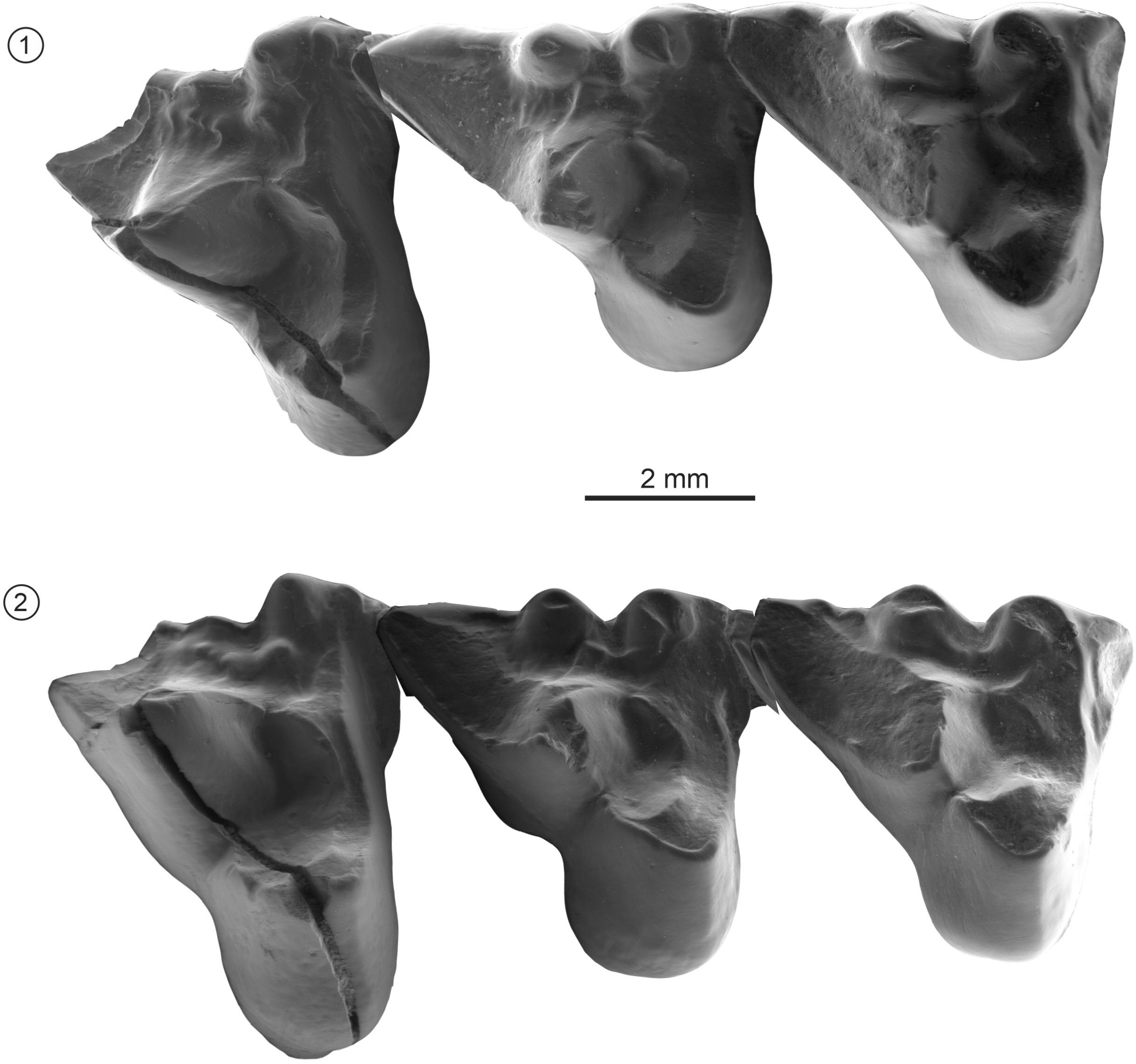

**Figure 3.** ***Lutreolina tonnii*** sp. nov. Scanning electron micrographs of the preserved molars (M1-3) of specimen **MLP 01-IV-5-29** (holotype). **1,** occlusal view; **2,** occlusal-lingual view. Scale= 2 mm.

Specimen MLP 01-IV-5-15, included in the hypodigm of the new species, is a right maxillary fragment with almost complete M1 and alveoli of P1-2 and dP3. The maxillary bone has preserved part of the lateral face, including the infraorbital foramen; in ventral view, it has preserved part of the hard palate, from almost its anterior edge to the anterior boundary of the palatal foramen. The alveoli of the dP3 are obvious in that they are extremely shallow as compared to those of the M1. The M1 is almost identical in size and shape to the homologous tooth of the holotype. Due to its better preservation, it can be observed a tiny StA cusp, as well as a very small and labio-lingually compressed StD.

**Comparisons with other Didelphini.** As mentioned, the combination of features in *L. tonnii* agrees well with that of the remaining species of the genus, contrasting with the condition seen in other Didelphini (with the exception of *Hyperdidelphys*; see below): in lateral view, the jugo-maxillary contact is subhorizontal in its posterior half; M4 is wider than M3; in M1-3 the centrocrista is shorter; there is a crest linking lingually the bases of StB and StD; a proportionally larger postmetacrista, and an anteroposteriorly compressed protocone which is more eccentric (anteriorly placed). Besides these differences, *L. tonnii* (as well as other species of the genus) has a deeper ectoflexus in M3 compared to the species of *Didelphis* Linnaeus, 1758. Differs from those of *Chironectes* Illiger, 1811, in being larger and in having similarly developed StB and StB in M1-2, and has a distinct crest linking their bases. Differs from species of *Philander* Brisson, 1762, in being much larger and in having a stronger posterior root of P3. Differs from species of *Thylophorops* Reig, 1952, in its size: larger than *T. perplana* Ameghino, 1904, smaller than *T. chapalmalensis* Ameghino, 1908, and much smaller than T. *lorenzinii* Goin *et al.*, 2009.

*Hyperdidelphys* is closer to *Lutreolina* than to any other Didelphini so far known (Goin & Pardiñas, 1996). *Lutreolina tonnii*, like other species of this genus, differs from those of *Hyperdidelphys* in that the carnivorous adaptations of its

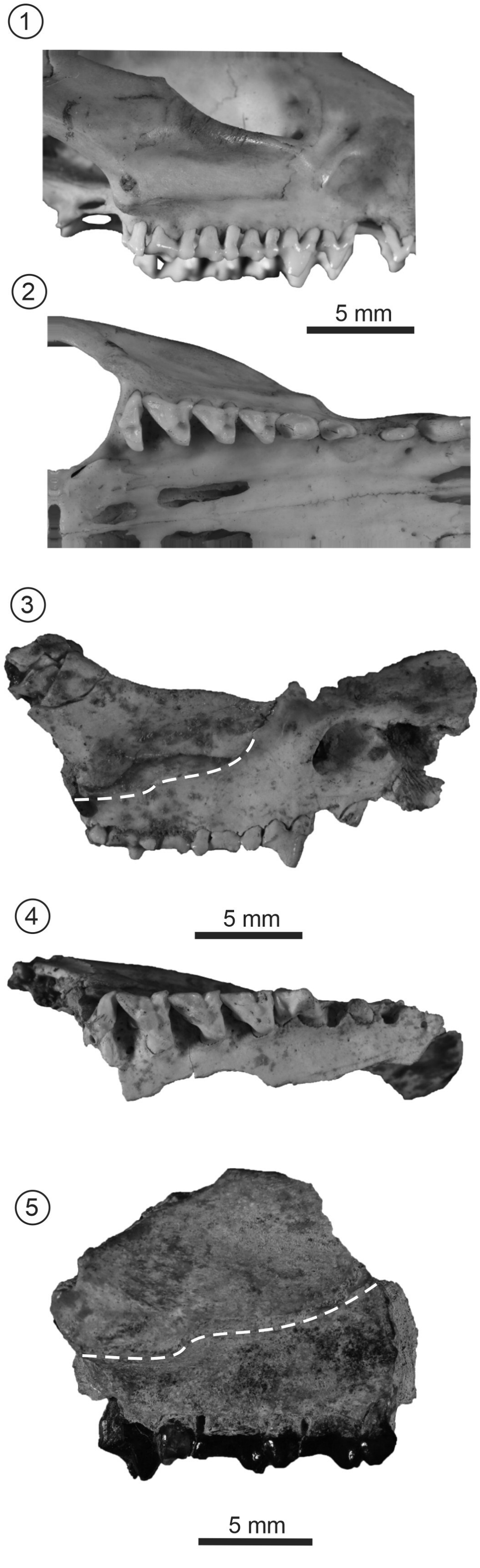

**Figure 4.** Lateral and ventral views of the maxillary bone in several species of ***Lutreolina***. **1–2,** ***L. crassicaudata***; specimen **MLP 707** in lateral (1) and ventral (2) views; **3–4,** ***L. tracheia***; specimen **MPC 4012-3** in lateral (3) and ventral (4) views; **5**, ***L. tonnii*** sp. nov., specimen **MLP 01-IV-5-29** (holotype) in lateral view. The dashed lines in **3** and **5** indicate the jugal-maxillary suture. Scale= 5 mm.

molars are less extreme than those of the latter: proportionally shorter postmetacrista, slightly smaller metacone, and less anteroposteriorly compressed protocone. Besides, it is larger than *H. inexpectata* Ameghino, 1889 and *H. parvula* Rovereto, 1914, slightly smaller than *H. pattersoni* Reig, 1952, and much smaller than *H. dimartinoi* Goin & Pardiñas, 1996. It has proportionally larger stylar cusps in M2-3 than *H. parvula*; proportionally smaller P3 (judging from the preserved posterior root of this tooth in *L. tonnii*) and larger StD in M2-3 than in *H. pattersoni*. Finally, differs from *H. dimartinoi* in having a proportionally larger StD in M2-3, a basal, lingual crest at the basal slopes of StB and StD, and in the absence of a small StC in the upper molars (though this feature is variable in *H. dimartinoi*). Goin and Pardiñas (1996) added several features of the lower teeth that also differ between *Lutreolina* and *Hyperdidelphys*: p2 is much larger relative to p3, and the lower molars have proportionally smaller hypoconulids, higher protoconids, and longer, more basined talonids with the cristida obliqua parallel to the labial edge of the tooth. Unfortunately, we cannot test these features in *L. tonnii* due to the lack of lower premolars and molars in the holotype and only (indubitable) referred specimen.

## DISCUSSION

### Tentatively referred specimens

As mentioned above, Goin and de los Reyes (2011) referred to *Lutreolina* sp. two specimens from Early Pleistocene levels (Ensenadan Stage/Age) of the coastal cliffs in southern Buenos Aires Province. One of them (MPH-P 070; Fig. 5) is a partial skull mostly lacking the rostrum, palate, and teeth (Fig. 5). The second one (MLP 01-IV-5-44; Fig. 6) is a fragment of dentary (posteriormost portion) lacking the teeth (Fig. 6). Both specimens are too large to be referred to any of the known species of the genus, though their preserved portions agree with their assignment to *Lutreolina*. On the other hand, both specimens match the size of *L. tonnii* but have no confrontable parts. Because of these reasons, here we only tentatively assign these remains to *L. tonnii*. Therefore, we keep them out of the hypodigm of this species.

**Figure 5.** Specimen **MPH-P 070**, a skull fragment lacking the rostral portion, tentatively referred to ***Lutreolina tonnii*** sp. nov. **1,** dorsal view; **2,** lateral (left) view; **3,** posterior view; **4,** ventral view. Modified from Goin and de los Reyes (2011, fig. 3A-D). Scale= 10 mm.

## Dental adaptations toward carnivory

It was already mentioned that a distinctive feature of the upper molars of *L. tonnii* is the important development of the postmetacrista. This trait is in tune with the (inferred or observed) more carnivorous feeding habits of representatives of both genera. Other features of the upper molar morphology also agree with their inferred feeding habits: closer para- and metacone (a geometrical consequence of the expanded postmetacrista), and anteroposteriorly compressed protocones (therefore, a reduced trigon basin).

Goin *et al.* (1992) performed a series of statistical analyses on the spatial orientation of the main cutting crests of the upper and lower molars in several living and extinct didelphids. They measured the angle of the paracristids in the lower molars, and of the postmetacristae in the upper ones relative to the dental axis. The rationale behind these measurements is that, in opossums with more carnivorous habits, the angular values would be lower, thus increasing the "scissors effect" of these antagonistic structures in occlusion. Accordingly, their results showed that didelphids with carnivorous feeding habits had lower angular values than those of omnivores or insectivores. For the upper molars, average angular values in the living *Lutreolina crassicaudata* were 37.7° (M1), 41.0° (M2), and 45.2° (M3) (angles invariably increase towards the rear end of the molar series). In contrast, opossums with omnivorous feeding habits had larger values: *Didelphis albiventris* Lund, 1840 had angles of 43.2° (M1), 46.7° (M2), and 50.5° (M3). Finally, the largest angular values were obtained in small opossums of mainly insectivorous habits: *Monodelphis dimidiata* Wagner, 1847 (48.7° in M1, 52.8° in M2, and 55.9° in M3); *Thylamys pusillus* Desmarest, 1804 (43.9° in M1, 49.5° in M2, and 54.9° in M3). Angular measurements for *Lutreolina tonnii* can only be made in the first two upper molars, as in M3 the metastylar corner of the tooth is broken. Values of M1-M2 are 39° and 40° respectively, quite close to those of the living *L. crassicaudata*. In *Hyperdidelphys inexpectata*, angular values are even lower: 37° (M1), 37° (M2), and 40° (M3; angles taken from Goin and Pardiñas, 1996, fig. 11E).

The spatial orientation of the main cutting crests is relevant to the understanding of the general molar geometry of upper and lower molars. For instance, the lesser the angle of the postmetacrista, the more eccentrically placed is the protocone, as the postprotocrista tends to align with the postmetacrista. Also, a large postmetacrista is usually associated with a short centrocrista, as the metacone is set closer to the paracone (see also Chemisquy *et al.*, 2015). For these reasons, "successful" dental designs tend to be conservative in evolution, thus explaining the similarities found in species of the same genus. Species of *Lutreolina* maintained their distinct molar design at least since the Late Miocene onwards, being *L. tonnii* its largest representative.

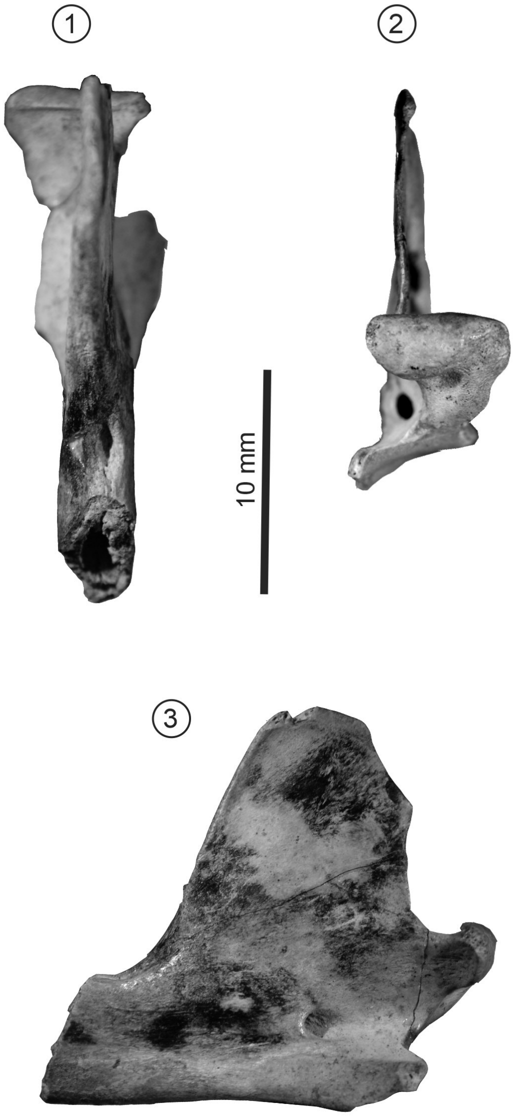

**Figure 6.** Specimen **MLP 01-IV-5-44**, tentatively referred to ***Lutreolina tonnii*** sp. nov.; an edentulous, posterior fragment of right dentary with the angular process, the ascending ramus, and the condyle. **1,** anterodorsal view; **2,** posterior view; **3,** lingual view. Modified from Goin and de los Reyes (2011, fig. 4A-C). Scale= 10 mm.

## Affinities between *Lutreolina* and *Hyperdidelphys*

It was already mentioned that, on the basis of the upper molar morphology, species of *Lutreolina* resemble those of *Hyperdidelphys* more than to any other didelphid. Goin and Pardiñas (1996) performed a phylogenetic analysis of the four species of *Hyperdidelphys*, also including *Philander opossum* Linnaeus, 1758, and *Lutreolina crassicaudata*. The resulting grouping was *Philander* (*Lutreolina* (*Hyperdidelphys* spp.)). The authors concluded that most synapomorphies shared by *Lutreolina* and *Hyperdidelphys* excluded other didelphines as well. Derived dental features that link both genera have already been mentioned (see above). To Goin and Pardiñas (1996), cranial features that support their affinities are the following: (1) in lateral view, the sagittal crest of both are straight (*i.e.*, almost horizontal), instead of bending upwards as in most remaining Didelphinae (*Metachirus* almost lacks a sagittal crest). (2) In *Lutreolina* and *Hyperdidelphys*, basicranial foramina—primary foramen ovale (*sensu* Beck *et al.*, 2022), carotid, and transverse canal—are placed very close to each other. In other didelphines, these foramina are set farther apart, especially the carotid one, which opens far more anteriorly. (3) The openings of the foramen ovale, carotid, and transverse canal shape a distinct triangle in *Lutreolina* and *Hyperdidelphys*, a feature absent in other didelphines. Finally, (4) the periotic promontorium is well-developed and pointed in species of both genera, while in other didelphines is less developed and has a more lamellar aspect.

## Diversity of *Lutreolina* in southern South America in the late Neogene

*Lutreolina tonnii* is the fourth extinct representative of this genus known to date. If the current taxonomy of the living species is not undervalued, extinct species double in number the extant ones. Three of the four extinct species (*L. tracheia*, *L. biforata*, and *L. tonnii*) come from localities placed south of Amazonia. The remaining one (*L. materdei*) was recorded in southeastern Peru, close to the western edge of Amazonia and not far from the Andean Cordillera. No extinct species of *Lutreolina* has been recovered in northern South America, though taking into account the scanty record in intertropical regions this could be due to a sampling bias. Notwithstanding, a workable hypothesis is that, contrary to previous statements by Castro *et al.* (2021), the *Lutreolina* (or *Lutreolina*-*Hyperdidelphys*) clade originated in mid-latitudes of southern South America to later disperse through more northern regions via the Andean corridor. An alternative hypothesis is that *Lutreolina* originated in the northern South American Llanos (partially coincident with the “Venezuela biogeographic area” of Castro *et al.*, 2021), also peripheral to the Amazonian region, to later disperse southwards also via the Andean corridor.

Goin (1989) suggested that two aspects characterized the evolution of South American Didelphoidea by the late Neogene: (1) a decided tendency towards the development of carnivorous types, some of them very specialized (*e.g.*, *Sparassocynus* Mercerat, 1898, *Hyperdidelphys*), and (2) a tendency towards an increase in their size. *Lutreolina tonnii* agrees quite well with both aspects. He also suggested that the final extinction of all of these specialized lineages was a consequence of the global cooling well underway by the Early–Middle Pleistocene (see also Goin *et al.*, 2016). The single occurrence of *Lutreolina tonnii* in southern South America happened, precisely, by Early Pleistocene times.

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